

STEREOTYPY AND VERSATILITY OF THE COPULATORY PATTERN OF *LYCOSA MALITIOSA* (ARANEAE, LYCOSIDAE) AT COOL *VERSUS* WARM TEMPERATURES

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ABSTRACT. Two groups of copulating pairs were observed, compared and analyzed. Ten copulations occurred in group A at cool environmental temperatures (mean = 16.2 °C). In group B, 10 copulations occurred at warm environmental temperatures (mean = 27.7 °C). Mean copulation duration of group A was longer than that of group B. However, both palpal insertion and palpal alternation numbers did not show any statistical differences between the groups. Temporal distribution of the palpal insertions, as well as the alternations in the use of each palp, showed differences in frequency and pattern when comparing the two groups. A high level of stereotypy of the copulatory behavior of *Lycosa malitiosa* was confirmed, together with the inverse correlation between duration and environmental temperature. The decision whether to switch from one palp to the other might be affected by temperature-influenced local factors, such as the viscosity of spermatid fluid and/or muscular fatigue in the palp.

The copulatory behavior of the lycosid spiders is generally complex and stereotyped. The palpal insertion patterns show few differences, if any, among closely related species, but these differences increase in importance at higher taxonomic levels. The following summary utilizes the classification of subfamilies proposed by Dondale (1986). One pattern consists of multiple consecutive hematochal expansions and contractions during a single palpal insertion; it is shown in species of Sosippinae (*Porrimsa lagotis*: Costa 1982), Venoniinae (*Pirata* sp., incomplete observation: Gerhardt 1924), Allocosinae (*Allocosa* sp., pers. obs.) and Lycosinae (*Lycosa thorelli* and *L. carbonelli*: Costa & Capocascal 1984; *Trochosa* spp.: Engelhardt 1964; *Alopecosa* spp.: Kronstedt 1979). A second palpal insertion pattern consists of the regular alternation of single insertions by each palp; this pattern is shown by species of Pardosinae (*Pardosa amentata*: Schmidt 1957; *P. nigriceps* and *P. pullata*: Bristowe & Locket 1926; *P. lapidicina*: Eason 1969; *P. ecatei*: Jiménez 1984) and Lycosinae (*Lycosa helluo*: Nappi 1965; *L. chaperi*: Sadana 1972; *L. rabida*: Rovner 1972; *L. tarantula fasciventris*: Ortega et al. 1986; *Lycosa* sp. from Uruguay: pers. obs.). The third and fourth patterns initially consist of a "series" of consecutive insertions with a palp, before alternating with the other palp. The third pattern is an alternating series

with each palp ending by none or few alternated single insertions, and has been described only in Lycosinae species (*Schizocosa* spp.: Montgomery 1903; Rovner 1973, 1974; Stratton & Uetz 1983). The fourth pattern is similar initially, but is followed by numerous alternating single insertions during much of the copulation period; and it has been described in some Uruguayan Lycosinae species (*Lycosa malitiosa*: Costa 1979; *L. poliostoma* group and *L. raptoria*, pers. obs.). Lycosinae stand out as the more diversified subfamily in relation to the copulatory pattern (polyphyly?).

Lycosa malitiosa Tullgren 1905 is a eurychronous spider species, with adult males and sexual activities present during the whole year (Costa 1979, 1991). Copulation consists of two phases of insertions (patterns) plus brief minor phases at the beginning and end (Costa 1979): initial phase, insertion phase I, insertion phase II, and final phase. The two insertion phase patterns represent 97.5% of the total copulation period, and include all the palpal insertions. Pattern I (PI) consists of multiple consecutive insertions with the same palp, change of side, then multiple insertions with the other palp, and so on. The number of consecutive insertions of each palp increases initially and thereafter gradually decreases with time. Finally, the male changes sides to carry out single insertions of each palp in the

alternate manner (Pattern II: PII). Chewing-like movements were always observed after each palpal insertion. On the average, PI lasts 40 min and PII lasts 60 min. However, Costa & Sotelo (1984) have noted that copulation duration in *L. malitiosa* changes according to environmental temperature variations (inverse correlation), much the same as what occurs in the physiological and developmental processes of poikilotherms.

The objective of this study was to determine whether environmental temperature variations could cause changes in the distribution of palpal insertions during copulation. The qualitative and quantitative characteristics of two groups of *L. malitiosa* maintained at different temperature conditions were compared and analyzed. Changes in a highly stereotyped behavior, as in the copulatory pattern of this species, could improve our knowledge on the mechanisms and factors which determine and control the sexual behavior of entelegyne spiders.

METHODS

Twenty males and 20 females of *Lycosa malitiosa* were collected as juvenile instars in the Marindia (Canelones, Uruguay). In the laboratory the spiders were individually raised in glass jars with sand, and mainly fed pieces of cockroach (*Blattella dubia*). Details of breeding methods were similar to those described in a previous paper (Costa 1979). In group A the spiders were raised in cool temperatures (range: 11–21 °C), and in group B the spiders were raised at warm temperatures (range: 22–33 °C). After molting, adult virgin spiders were divided into two groups. In group A, 10 males mated only once with 10 females at cool temperatures (winter season: June to September). In group B, 10 males mated only once with 10 females at warm temperatures (summer season: December to February). Other environmental conditions such as humidity, lighting, and photoperiod were maintained relatively constant.

The following copulatory characteristics were recorded in detail: number of insertions performed for each active palp, number of side changes (alternation in the use of palps), number of bouts of chewing-like movements of the just-used palp, together with the durations of insertions and side changes. The total copulatory duration was timed from the male's mounting of the female until the dismount (see Costa 1979).

The Student *t*-test and Mann-Whitney *U*-test

Table 1.—Copulation duration in *Lycosa malitiosa* and environmental temperature in Groups A (10 pairs) and B (10 pairs). Mean values and standard deviations (SD) are shown together with results obtained when using Student's *t* test to compare them. CV: coefficient of variation; *P*: probability.

	Copulation duration (min)		Temperature (°C)	
	Mean \pm SD	CV (%)	Mean \pm SD	CV (%)
Group A	127.2 \pm 29.7	23.3	16.2 \pm 1.5	9.3
Group B	80.2 \pm 13.4	16.7	27.7 \pm 1.5	5.4
<i>t</i> test	4.56		17.14	
<i>P</i>	<0.001		<0.001	

were used for statistical comparison between groups. The limit of statistical significance was set at *P* = 0.05. The curves shown in Fig. 1 were fitted using the polynomial regression programs from the PRESTA statistical package (Centro Ramon y Cajal, Madrid, Spain).

RESULTS

Mean values of copulation duration (CD) from group A (cool) were significantly higher than the values obtained in group B (warm). Mean environmental temperature values also differed when comparing the two groups (Table 1). A large variation in CD values in group A coincided with the large variation of its temperature values.

Values of palpal insertion number, number of side (palpal) changes, duration, insertion frequency, and side change frequency of insertion patterns (PI and PII) in groups A and B were compared (Table 2). Significant differences were found in total values (PI + PII) durations as well as insertion and side change frequencies. No differences in total values for insertion numbers and side change numbers were found between the groups. However, side changes in group A occurred more often than in group B when considering only PI. In PII, insertion and side change numbers from group B were higher than in group A. Differences in duration and frequency were maintained between groups in both the PI and PII (Table 2).

Differences in the number of insertions per series were found between the two groups when considering only the PI values. Group A performed 13.7 (\pm 4.5 SD) insertions per series, whereas group B performed 20.3 (\pm 2.8 SD) in-

Table 2.—Palpal insertions and side shifts during the main copulatory phases in groups A and B. Mean values and standard deviations (SD) of the whole behavior; main pattern I (PI) and main pattern II (PII) are shown separately. Results obtained when applying the Student's *t* test (PI + PII duration values) and the Mann-Whitney *U* test (numbers and frequencies) to compare the two groups are also shown. *P*: probability.

	Number of insertions	Side shift number	Duration (min)	Insertion frequency	Side shift frequency
	Mean \pm SD	Mean \pm SD	Mean \pm SD	Mean \pm SD	Mean \pm SD
<i>PI</i>					
Group A	224.7 \pm 53.0	17.4 \pm 5.3	55.1 \pm 16.0	4.2 \pm 0.6	0.3 \pm 0.1
Group B	242.9 \pm 63.2	11.9 \pm 2.9	24.0 \pm 4.9	10.2 \pm 1.8	0.5 \pm 0.1
Test	<i>U</i> = 47.5	<i>U</i> = 17.5	<i>t</i> = 5.88	<i>U</i> = 2.0	<i>U</i> = 11.5
<i>P</i>	N/S	<0.02	<0.001	<0.002	<0.02
<i>PII</i>					
Group A	40.2 \pm 10.1	40.2 \pm 10.1	68.5 \pm 18.0	0.6 \pm 0.2	0.6 \pm 0.2
Group B	60.1 \pm 18.8	60.1 \pm 18.8	52.9 \pm 11.0	1.1 \pm 0.3	1.1 \pm 0.3
Test	<i>U</i> = 19.0	<i>U</i> = 19.0	<i>t</i> = 2.34	<i>U</i> = 8.5	<i>U</i> = 8.5
<i>P</i>	=0.02	=0.02	<0.05	<0.002	<0.002
<i>Totals</i>					
Group A	265.0 \pm 57.2	57.6 \pm 13.5	123.6 \pm 30.5	2.2 \pm 0.3	0.5 \pm 0.1
Group B	303.5 \pm 67.3	72.0 \pm 19.0	76.9 \pm 13.2	4.0 \pm 0.9	0.9 \pm 0.2
Test	<i>U</i> = 36.0	<i>U</i> = 28.0	<i>t</i> = 4.56	<i>U</i> = 9.5	<i>U</i> = 3.5
<i>P</i>	N/S	N/S	<0.001	<0.002	<0.002

sertions per series, (*U* = 14, *P* < 0.02). Palpal insertion distribution showed some differences between the groups (Fig. 1). In group A, a moderate number of insertions per series was distributed among several series; in group B, a high number of insertions per series was distributed among few series. Figure 1 summarizes the different curve shapes of PI in the two groups.

The bouts of chewing-like movements showed no significant differences between groups when using the *U*-test in both CI (3.98 \pm 0.68 in A and 3.46 \pm 0.51 in B) and CII (4.89 \pm 1.34 in A and 5.82 \pm 1.33 in B).

DISCUSSION

Lycosa malitiosa copulating at a cool temperature have a higher copulation duration than do those at a warm temperature. This is in agreement with the inverse correlation between CD and environmental temperature found by Costa & Sotelo (1984). New experimental data (Costa & Sotelo, unpubl.), in which other environmental factors were kept constant, support this probable influence of temperature.

The absence of differences between groups in the total numbers of palpal insertion and side change suggests that both parameters are species-

specific characteristics of *L. malitiosa*, in spite of the drastic changes found in copulation duration. The numerical constancy of behavioral acts, and the temporal changes induced by temperature variations, are consequently responsible for the changes in frequency of palpal insertion and side shift. On the other hand, the overall specific copulatory pattern should remain unaltered, showing the usual succession: initial phase, insertion phase I and II, and final phase (Costa 1979). However, the distribution of the behavioral units proved to be sensitive to temperature changes (differences in side change number in PI and PII, insertion number in PII, as well as in the curves of distribution of insertions per series).

Subtle behavioral changes probably can not be explained by a direct influence of environmental temperature over the nervous centers which control this behavior. At least two physiological processes could be responsible for these variations at the palpal level: fatigue of muscles related to functioning of the genital bulb and/or changes in the viscosity of spermatid fluid in the palpal duct.

Fatigue of a valvular opening muscle located in the male palp, allowing hemolymph flow into the hematodocha, was postulated by Rovner (1975) to account for the progressive increment

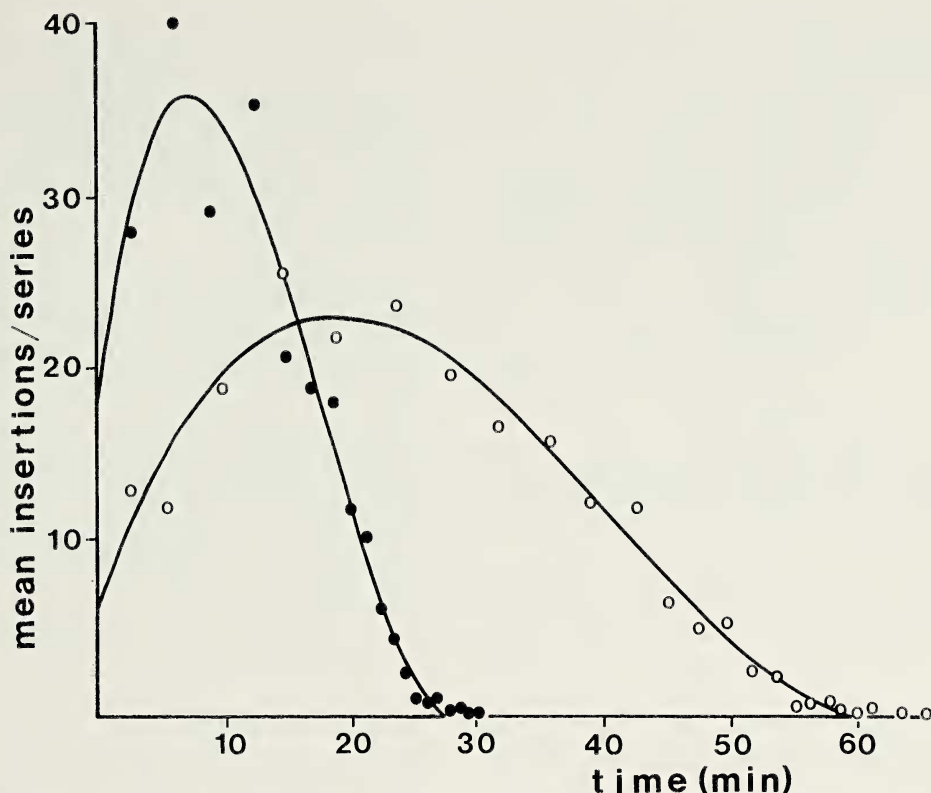


Figure 1.—Main copulatory Pattern I (PI) of the two groups of *Lycosa malitiosa*. The temporal insertion distribution per series was established by obtaining average values for each consecutive series in each group (Group A: open circles - \circ ; Group B: dark circles - \bullet). The curves were fitted according to the polynomic regression program of the PRESTA statistical package.

of palpal insertion duration in entelegyne male spiders. This hypothesis was supported by previous findings by the same author (Rovner 1971, 1972, 1974; Rovner & Wright 1975) in *Lycosa rabida*, *Schizocosa saltatrix* and *S. avida*. This palpal muscle would be more efficient at a higher environmental temperature than at a lower one (for example, by improving flow rates), thus enhancing the number of consecutive insertions.

Our hypothesis proposes a proprioceptive input from the palp, which could indicate the diminution or absence of the spermatic fluid. This process would be altered by temperature variations. At cool temperatures the fluid would be more viscous than at warm and would flow slowly into the spermophor (palpal duct). Putative spermophor receptors could initiate an early side change due to the decrease or absence of fluid. At warm temperatures the spermatic fluid would flow rapidly, delaying the side shift and

therefore resulting in a higher number of consecutive insertions of each palp. PII would be triggered by a major depletion of sperm fluid in the spermophor, while a single insertion would trigger the side shift and use of the other palp. Current studies suggest that the presence of fluid in the spermophor, and not necessarily sperm, is responsible for this phenomenon.

The hypotheses presented above do not exclude one another. The male could make the decision to switch palps when spermatic fluid is scarce or absent in the sensitive region of the spermophor and/or when the valvular muscle is fatigued. Both neural programming and the presence of spermatic fluid in the opposite palp could trigger the palpal shift. Higher temperatures could facilitate a better fluid evacuation and/or a better action of the valvular muscle, thus accounting for the slightly higher number of palpal insertions and side shifts performed by

group B. Variations in copulatory behavior due to environmental temperature would always be buffered by genetic constraints.

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